

The Pre-Pliocene Tennessee River and Its Bearing on Crawfish Distribution (Decapoda: Cambaridae)

J. F. FITZPATRICK, JR.

*Department of Biological Sciences,
University of South Alabama, Mobile, Alabama 36688*

ABSTRACT.— Recent demand for fossil fuels has provided opportunities for extensive and detailed examination of surface and subsurface unfossiliferous clastic deposits of the Coastal Plain of the Gulf of Mexico. Among the new discoveries is an ancient outlet directly into the Gulf for the upper Tennessee River more than once during mid- and late Tertiary times. Also discovered is evidence that the intrusion of the Mississippi Embayment apparently occurred much later than implied by surface outcrops in Mississippi and Alabama. Many Cambaridae distribution patterns show close associations with these Tertiary deposits; included are *Cambarellus*, *Fallicambarus*, *Faxonella*, *Hobbsseus*, *Procambarus* (*Acucauda*), *P.* (*Girardiella*), *P.* (*Leonticambarus*), *P.* (*Pennides*), and *P.* (*Scapulicambarus*). Some possible interpretations relating to these distributions are discussed, as is the pattern of *Orconectes* and *Cambarus* invasion. Much detailed study is badly needed, and potentially fruitful areas for investigation are indicated.

The earliest attempts to explain the population of North America by cambarid crawfishes were based on the assumption of a Mexican epicenter, from which the major groups radiated to invade the United States and Canada, east of the continental divide. This was probably best articulated by Ortmann (1905). Subsequently, however, Hobbs has presented a cogent and compelling series of arguments in favor of an origin in the southeastern United States (1958, 1962a, 1967, 1969, 1981, 1984; Hobbs and Barr 1972). Probably his best statements appeared in his treatment of the Pictus Group of *Procambarus* (1958) and his masterly analysis of *Cambarus* (1969). He continued his strong contentions in a monograph of Georgia species (1981) and an analysis of the distribution of *Procambarus* (1984).

Although a detailed analysis of phylogenetic relationships is inappropriate here, it does seem worthwhile to review some of the major trends. Most of these are based on Hobbs. A *Procambarus*-like ancestor is generally accepted, and indeed no one has taken issue with Hobbs's contention that the Pictus Group of the subgenus *Ortmannicus*, of all extant species, is most like the ancestral form (1958). He has, however, recently (1981, 1984) added that certain members of the subgenus *Pennides* are among the most primitive. Although he has somewhat revised his concepts of relationships (1972, 1981, 1984), Hobbs has retained

much of the phylogeny of *Procambarus* that he expressed in his review of the Blandingii Section (1962a). Two of his "Groups" in that paper were elevated to subgenera in 1972, with the remaining species of the Section being assigned to the subgenus *Ortmannicus*. It is important to reemphasize in this paper that certain members of the subgenus *Pennides* (formerly the Spiculifer Group of the Blandingii Section) possess many of the "primitive" characters assigned to the "ancestral procambarid" (multiple cervical spines; short, broad areola; strongly acuminate rostrum; "striped saddle" pattern of coloration; male first pleopod with full complement of terminal elements, those elements relatively simply constructed; etc.). One must likewise keep in mind that in the Cambaridae the male and female organs associated with sperm transfer are the most—and sometimes only—reliable taxonomic characters; one can develop good concepts of initial (i.e., early) plesiomorphies in other characters/structures, but they are all subject to considerable convergence or modification in response to environmental habits, making determination of synapomorphies nearly impossible.

Considerable data are accumulating to indicate that the "upper Tennessee" river had independent access to the Gulf of Mexico at least as recently as the early Pliocene. This new interpretation does not refute the phylogeny of the Cambaridae accepted by the more recent workers, but it does require reexamination of temporal assignments for events. Certain zoogeographic confusions are partially resolved. Alternate explanations to those currently accepted are proposed to (1) account for the distribution of the early-emerging Cambarellinae, (2) elucidate the existence of "primitive forms" of the subgenera *Pennides* and *Ortmannicus* of *Procambarus* in their present geographic distribution, (3) suggest the origin of the subgenus *Scapulicambarus* as being in lower Georgia in pre-Miocene times, (4) propose that the spread of the genus *Fallicambarus* east of the Mississippi River is post-Miocene, (5) place the origin of the genus *Faxonella* in central Louisiana during the Eocene, (6) identify the origin of the genus *Hobbseus* as eastcentral Mississippi during the Eocene, and (7) suggest pre-Eocene origins for the genera *Orconectes* and *Cambarus*, with their spread into the area of the Mississippi Embayment occurring only relatively late in geologic time.

PHYLETIC AND ZOOGEOGRAPHIC OVERVIEW

The genera *Barbicambarus*, *Cambarus*, *Distocambarus*, *Fallicambarus*, *Faxonella*, *Hobbseus*, *Orconectes*, and *Troglocambarus* have been demonstrated to be derivatives of the ancestral procambarid (Hobbs 1967, 1969, 1981). Hobbs, however, did not visualize a more or less lineal descent with a simple cladistic dichotomy. Instead, he postulated radiate evolution in which some *Procambarus*, principally eastern species, arose at one level of the tree and diversified, and a second, somewhat later in time, series of diversifications in one of the stem

stocks organized around an adorconectoid stock. (Mexican diversity, especially interesting to a zoogeographer, is outside the realm of this treatment.) From the former (earlier) populations we see today members of the subgenera *Capillicambarus*, *Hagenides*, *Lonnbergius*, *Ortmannicus*, *Pennides*, *Scapulicambarus*, *Tenuicambarus*, and *Villalobosus*, plus the genus *Troglocambarus*.

From the adorconectoid line (later temporally), stocks developed that culminate in the procambarid subgenera *Acucauda*, *Austrocambarus*, *Girardiella*, *Leonticambarus*, *Mexicambarus*, *Paracambarus*, *Procambarus*, and *Remoticambarus*, plus the genera *Barbicambarus*, *Cambarus*, *Distocambarus*, *Fallicambarus*, *Faxonella*, *Hobbseus*, and *Orconectes*. One of the more striking features of the latter assembly is that, except for *Cambarus* and *Distocambarus*, geographically they are more or less western (in relation to the proposed center of origin of the cambarines). Although not a complete "family tree" for the Cambaridae, Figure 11 of Hobbs's Georgia monograph (1981) is adequate to demonstrate his ideas. He does not visualize polyphyletic origins; instead, he sees the non-procambarid genera as widely divergent stocks that originated from divers stocks of *Procambarus*. (The groupings as I have made them fundamentally rest on Hobbs, as I have cited him; but if they prove to be non-congruent to his concepts, the fault is entirely misinterpretation on my part.) This latter adorconectoid line seemed to be the less conservative of the two main *Procambarus* stocks, as evidenced by the extremes—recognized as genera—of apomorphies developing in it.

Another early divergence from the cambarine-procambarid stock resulted in the monogeneric Cambarellinae. Hobbs' last lengthy discussion of this phylogeny (1969) was concerned with establishing the relationships between the Cambarinae and the Cambaroidinae, taking for granted an understanding of the close association of the former and the Cambarellinae. More recently, Fitzpatrick (1983) addressed the infrageneric relationships of the members of *Cambarellus* and tried to establish their phylogenetic affinities with other Cambaridae. The dwarf crawfishes are also basically western in distribution.

The determination of these lineages did not, however, afford non-moot concepts and explanations of current distributions. Indeed there are many enigmas and paradoxes. Among these are the geographic ranges of those *Cambarellus* most like the ancestral form, and an explanation of why the culminations of an early offshoot of cambarine evolution would be excluded from the proposed ancestral home. Yet they seem to be highly competitive and successful against advanced (and therefore, competitively selected) members of groups that emerged at a later date (Penn and Fitzpatrick 1962, 1963).

Members of the subgenus *Pennides* have many characters attributable to the "ancestral procambarid": a full complement of simple terminal elements on the male pleopod; multiple carapace spines; a short,

broad areola; the shape of the rostrum, chela, carapace and pereopodal coxae; and color pattern. In the subgenus there are two principal assemblages, not formally recognized by Hobbs (1972). In one group, a full complement of terminal elements is present on the gonopod; in the other (*gibbus*, *raneyi*, *spiculifer*) the cephalic process is absent; in *P. (Pe.) ouachitae* Penn the cephalic process is also sometimes absent.

I am not sure that Hobbs would still believe that *P. (Pe.) vioscai* Penn is the most "primitive" extant species of the subgenus, but there is no doubt that a reduction in terminal elements is apomorphic. Of the three species so disposed, all are found in the most eastern part of the range of the subgenus, while species with a full complement of terminal elements also found in that part of the range have quite specialized pleopods and annuli ventrales (Fig. 1). The more generalized species are found from Mississippi westward.

Populations of *P. (Pe.) ouachitae* (or siblings) occur allopatrically in Arkansas and Mississippi. This species seems to be morphologically intermediate between species with the full-complement of terminal elements and those with a short-complement. Further, the populations of *P. (Pe.) vioscai* that occur east of the Mississippi River have a much more modified cephalic process than those west of the river. They are sufficiently different that work I have in progress will probably result in my proposing subspecies categories for the two forms. The siblings, *P. (Pe.) penni* Hobbs and *P. (Pe.) clemmeri* Hobbs, are so distributed that the more eastern form is also the more remote (from the ancestral type) form (Fitzpatrick 1977a). The entire picture suggests an invasion of the lower Gulf Coastal Plain by an early offshoot of *Procambarus* stock, and subsequent reinvasion of the southeastern United States along corridors located near the present coastline (Fig. 2).

Except for the nearly unique subgenus *Lacunicambarus*, which Hobbs (1969:163) believed to have been "one of the earliest branching stocks," *Cambarus* is represented in the central Gulf area only by *C. (Depressicambarus) striatus* Hay. Bouchard (1978) assigned this species to the superspecific assemblage he considered the more advanced, yet one must remember that Hobbs (1969) believed *Depressicambarus* to represent a moderately early digression in cambarid evolution. Hobbs (1969:169) conceded that his proposed dispersal corridors to this region, especially for *Lacunicambarus*, are tenuous.

The representatives of *Orconectes* in the area are all members of specialized and advanced Virilis and Palmeri Groups. Except for *Falli-cambarus fodiens* (Cottle) and *F. uhleri* (Faxon), all members of that genus occur on the Gulf Coastal Plain or in reasonable proximity to its central and western parts. Further, the most primitive species lie in southwestern Louisiana and southwestern Arkansas, "probably not far from the ancestral home of the genus" (Hobbs 1969:124). The most "primitive" *Faxonella*, *Fx. creaseri* Walls, is found in northcentral Louisiana, while *Hobbseus* is confined to the middle and upper Tombigbee

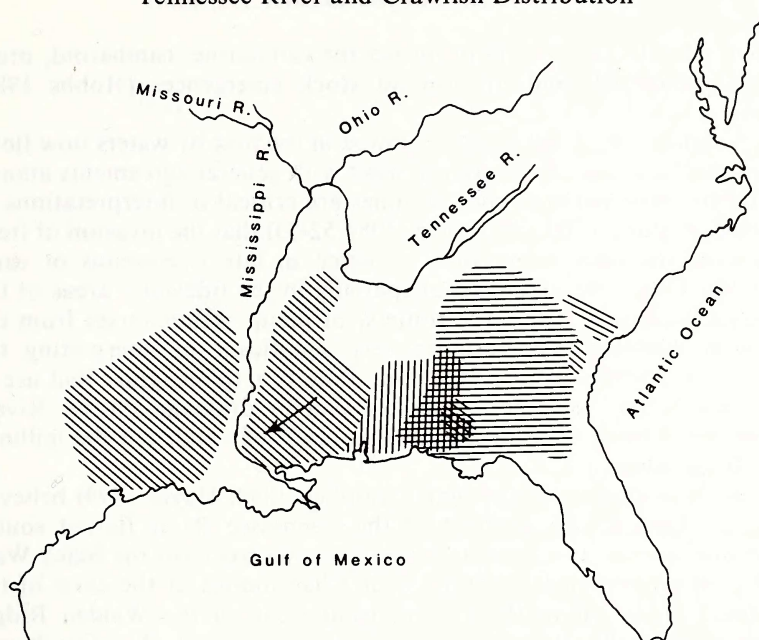


Fig. 1. Distribution of *Procambarus* (*Pennides*). Arrow designates route of proposed "Miocene Tennessee River." Diagonal rulings = cephalic process present; horizontal rulings = cephalic process absent; vertical rulings = *P. (Pe.) versutus*.

River drainage (proper) and the upper part of the Pearl River drainage (Fitzpatrick 1977b). Clearly, then, considerable diversity of cambarine crawfishes seems to have originated in a secondary center associated with the lower reaches of the Mississippi River and its environs, markedly distant from the "southeastern" primary center envisioned by Hobbs (loc. cit.). An enigma of how the several populations became established there presents itself. Since this is not a taxonomic paper, it seems improper to continue a discussion of detailed relationships; besides, Hobbs (1967, 1969, 1981, 1984) has explained well our current knowledge of phylogenies. Instead, I propose to examine geographic and geologic information, particularly some recently collected data, which could assist in resolving some of the apparent paradoxes of crawfish distribution.

GEOLOGIC CONSIDERATIONS

Classical thinking by crawfish workers (and many others) establishes a thesis that, during some pre-Pleistocene period, the upper and lower portions of the Tennessee River were separate. Faunal comparisons certainly seem to indicate this. The upper basin is more intimately

associated with the centers proposed for cambarine, cambaroid, orconectoid, graciloid, and mexicanoid stock emergences (Hobbs 1981, 1984).

Although the exact routes followed in the past by waters now flowing in the Tennessee River do not meet with general agreements among geologists, their paths at specific times are critical to interpretations of crawfish evolution. Hobbs argued (1981:52-53) that the invasion of fresh waters by the cambarine stock occurred in late Cretaceous or early Cenozoic times. He placed them spatially in the tidewater areas of the extreme Southeast. Thus, the route(s) of major watercourses from the southern Appalachians becomes very significant in interpreting the invasion of North America. It is important, too, to recognize that use of the word "river" here designates a basin or drainage source. Rivers themselves have lives measured in thousands of years, not the millions of geologic times.

Some geologists (Hayes and Campbell 1894, Hayes 1899) believed that the Appalachian segment of the Tennessee River flowed southwestward through the present Coosa-Alabama basin (or the Black Warrior). They envisioned a capture near Chattanooga at the close of the Tertiary, which led to the present transection of the Walden Ridge. Zoogeographically, this would seem to be supported. A major faunal break seems to be associated with the Walden Gorge.

Some geologists (Johnson 1905, Wright 1936) believed otherwise. They insisted that the present route of the Tennessee River has existed at least since the Schooley (dissection of the peneplain ending probably in the Miocene). The geological evidence to support this thesis is of equal strength as that supporting the one of Hayes and some subsequent authors. The Tennessee remains a difficult problem. A good review is in Thornbury (1965:124-126).

Sedimentary analysis of Mississippi "Eocene" deposits by Grim (1936), however, provided compelling data to indicate the delta of a sizeable river in eastcentral Mississippi. The Midway alluvial deposits (Paleocene) (Fig. 3) indicate that a significant river had a delta in the vicinity of the Chickasaw-Clay counties area near the juncture of the Porter's Creek and Clayton formations. The succeeding Wilcox deposits (early Eocene) (Fig. 4) demonstrate the continuance of this river into the Choctaw-Montgomery-Webster counties area. Grim (p. 208) attributed both the Midway and Wilcox deposits to a "complex of ancient rocks located in the present Piedmont Plateau." The Claiborne deposits (mid-Eocene), in contrast, suggest that "many streams" (p. 214) rather than one contributed to them. Similarly, the post-Claiborne Jackson Formation (late Eocene) indicates the major "Appalachian [= Tennessee] River" was not a controlling depositional factor in Mississippi.

Brown (1967) was concerned over an apparent inconsistency of the major streams of southern Mississippi. Contrary to other Recent drainage patterns, they flow at a decided angle to the dip and strike of the

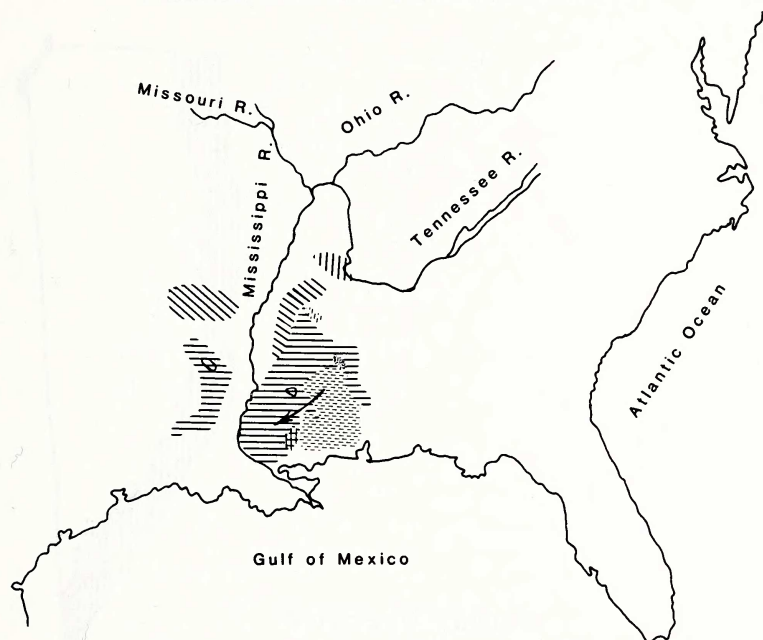


Fig. 2. Distribution of western species of *Procambarus* (*Pennides*). Arrow as in Figure 1. Solid vertical rulings = *P. (Pe.) ablusus*; broken vertical rulings = *P. (Pe.) lylei*; solid horizontal rulings = *P. (Pe.) ouachitae*; broken horizontal rulings = *P. (Pe.) clemmeri*; cross-hatching = *P. (Pe.) penni*; stippling = *P. (Pe.) lagniappe*; enclosed by open circles (2) = *P. (Pe.) elegans*.

"Miocene" belt. Northeast trending fluvial ridges, which form a drainage divide, readily explain the disparity (Fig. 5). The underlying deposits that defend the ridges are mapped as Citronelle Formation (Pliocene-Pleistocene). (It should be noted that many geologists question the accuracy of equating the Mississippi-Alabama Citronelle with the formation of the same name farther to the east in Florida and to the west in Louisiana.) Brown's analysis of the gravels led him to postulate the existence of a "very large river flowing southwestward" (p. 82), the gravels forming a part of that river's bed.

New studies, using different and more modern techniques, have helped resolve some of these problems. An important aspect of contemporary geology, especially along the Gulf Coastal Plain, is the greatly expanded search for fossil fuels. Geologists are no longer confined to outcrops as sources of stratigraphic data. Indeed, the economic considerations of the petroleum industry have mandated an intensive study of subsurface formations and expanded drilling activities. The masses of new information have transformed the study of the Coastal Plain into a rapidly evolving, incessantly refined activity. Along with this have come many reevaluations of the relationships between stratigraphic series,

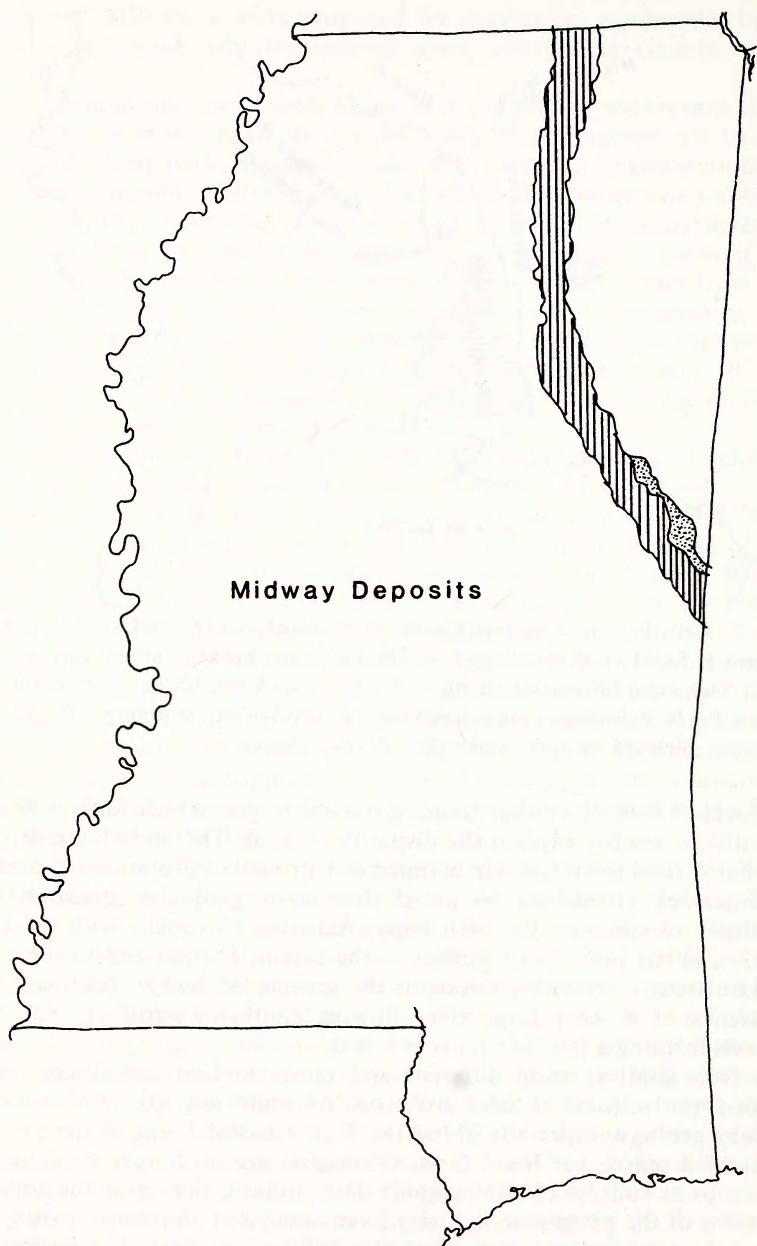


Fig. 3. Midway deposits in Mississippi. (Redrawn from Grim 1936.) Vertical rulings = Porter's Creek Formation; stippling = Clayton Formation.

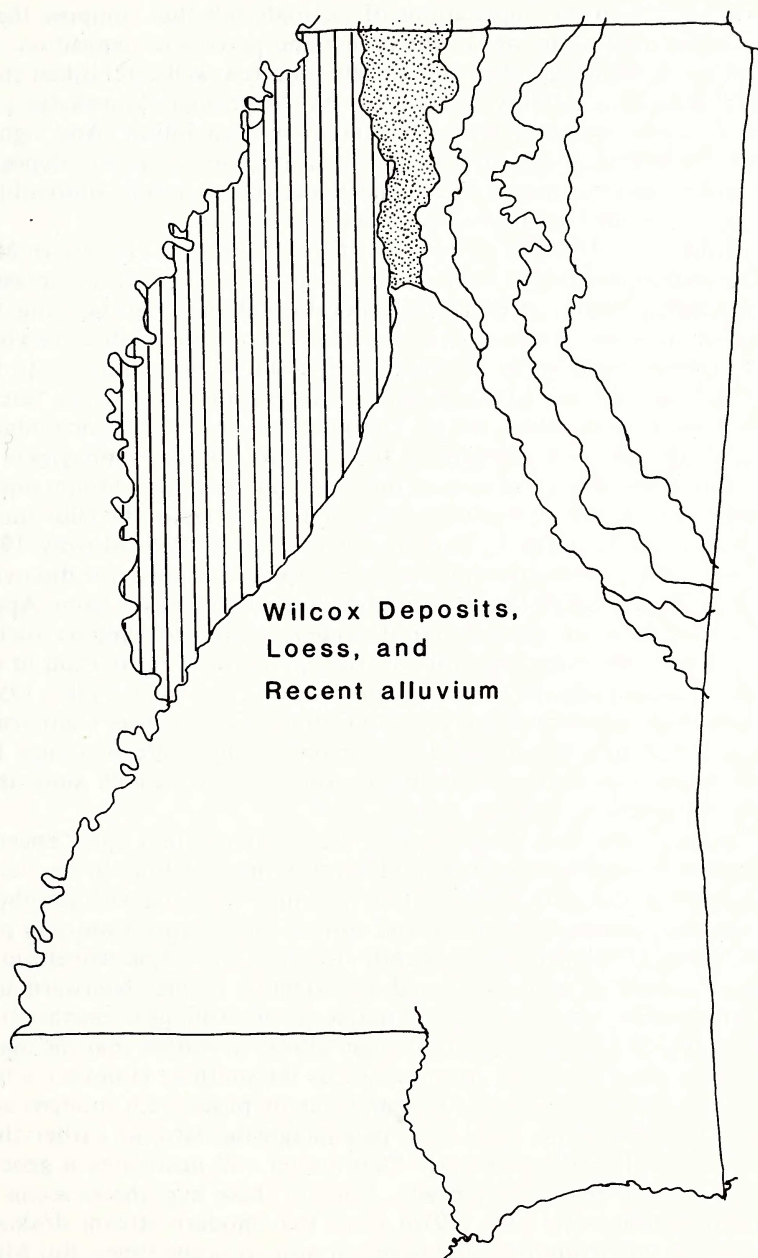


Fig. 4. Wilcox, loess, and river alluvium in Mississippi. (Redrawn from Grim 1936). Vertical rulings = recent river alluvium; stippling = loess, loam, gravel, etc.; other lines delimit the several formations of the Wilcox deposit.

interpretations of the implications of the materials that compose them, and clearer understandings of the events and periods of deposition. No longer is the zoogeographer able to rely on a few well-established studies and assume a stability of concept. As the geologic knowledge progresses, so the zoogeographic interpretations must follow. And significant modification of age, stratigraphic relationships, sources of deposits, and biological responses is to be expected as the essentially unfossiliferous clastics of the Gulf Coastal alluvia are examined.

Isphording (1981), working with drill cores from southwestern Mississippi and especially in the Hattiesburg Formation (Miocene), amassed considerable, nearly irrefutable mineralogical data establishing the existence in Miocene times of a river that entered the Gulf somewhere near Hattiesburg (Fig. 6). Further, these data tie the sediments to the eastern Piedmont and southern Appalachians rather than to the "local" source areas (Isphording 1983). The mineralogical suites encountered are incompatible with weathering from the Mississippi Embayment to the north of the collecting sites or the more remote Rocky Mountains or Central Interior, which had been suggested as sources of the alluvium of the central Embayment by earlier writers (Storm 1945, Murray 1955, MacNeil 1966). Such a river, if not the Tennessee, requires the discovery of yet another river of equal magnitude draining from the same Appalachian source area. No geological evidence exists to support such a thesis. Even more data are available to support the contribution of the southern Appalachians to the Embayment. Todd and Folk (1957), working with sediments from Bastrop County, Texas (lower Claiborne), reported that they encountered a kyanite-sauroilite suite that they felt could come only from the southern Appalachians, which suite they called "diagnostic" (p. 2560).

Isphording (1981) and Brown (1967) implied that the "Eocene" deposits of Grim (1936) were possibly misleading in dating the demise of the last Tennessee outlet directly into the Gulf. Working with geophysical logs and clastics, subsurface and surface, and mapped outcrop patterns, May (1981:29) independently reached the same conclusions: "Miocene outcrop patterns should be extended further landward into the Embayment," in Mississippi. Analyses from drillings in northcentral Mississippi led Murphey and Grissinger (1981) to believe that the materials under the Pleistocene loess mantle as far south as Holmes County suggest an erosion surface, frequently out of phase with modern surfaces. They placed the age, from paleomagnetic data, at earlier than 700,000 B.P. (late Pliocene-early Pleistocene) and postulated a general "Citronelle" age for these deposits. None of these hypotheses seems to be incompatible with Alt's (1974) ideas that modern stream drainage patterns (*on the Atlantic coast*) began in post-Miocene times. But Murphey and Grissinger's (1981) conclusions indicated clearly that modern drainage patterns in the upper Embayment are unreliable indicators of history before the late Pleistocene.

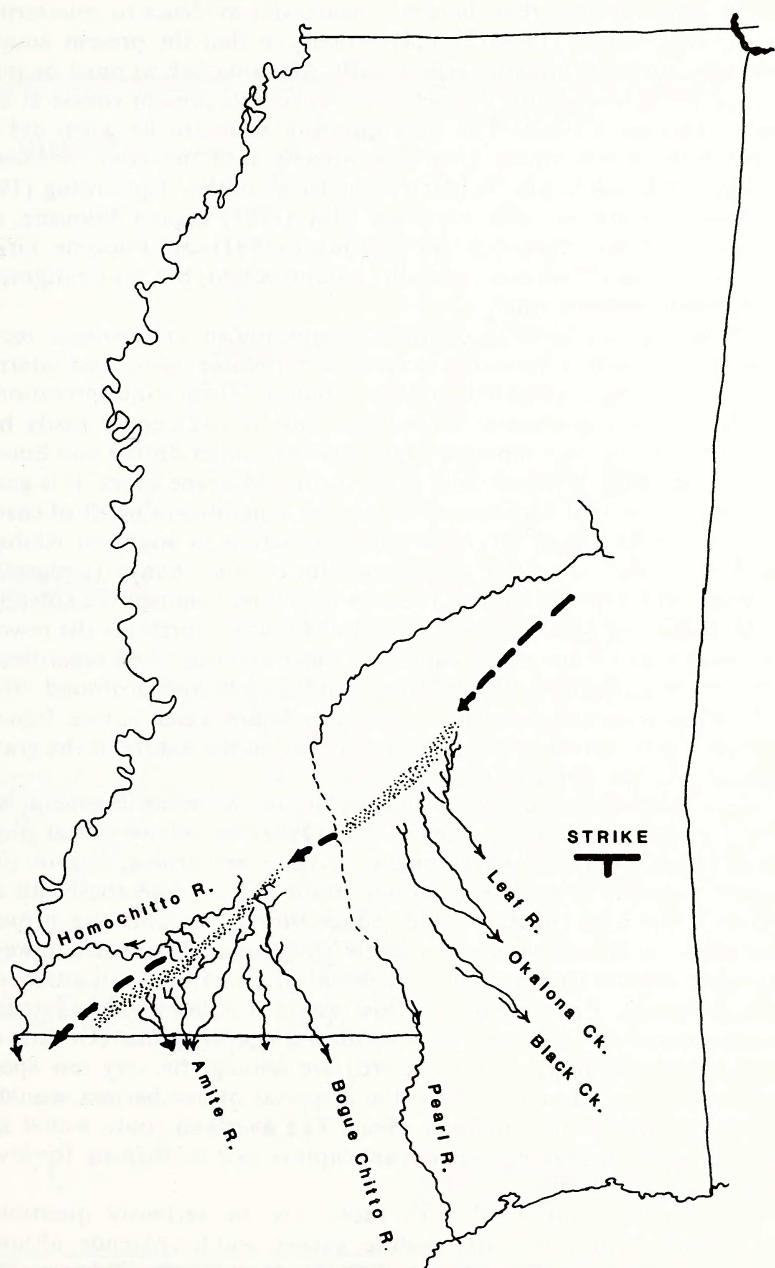


Fig. 5. Proposed Miocene "Tennessee River." (After Brown 1967.) Stippling = gravel-defended ridges; broken arrows = proposed route of river.

It appears, then, that there is considerable evidence to counterindicate Smith-Vaniz's (1968:122-124) contention that the present zoogeographic pattern of aquatics (specifically Alabama fishes) must be interpreted on the basis of the Tennessee occupying its present course at least since Cretaceous times. The only question seems to be when did the connection of the upper Tennessee directly into the Gulf of Mexico become replaced by the indirect Ohio River outlet. Isphording (1981) claimed Miocene or early Pliocene; May (1981) argued Miocene; and Brown (1967) and Murphey and Grissinger (1981) said Pliocene. Grim's Eocene datings (1936) seem possibly compromised, but his stratigraphic relationships remain valid.

Equally, one must recognize that nothing in the geologic record requires continuous discharge through a particular basin, and intermittent flow remains a viable hypothesis. Indeed, Grim's interpretation of Claiborne sediments seems to indicate this. A river could easily have accounted for Grim's deposits, found another outlet during late Eocene, and reestablished a direct Gulf outlet during Miocene times. It is generally recognized that Miocene is the date of a significant uplift of eastern North America. Even the Citronelle Formation in southern Alabama exhibits a "tilt" to reflect the magnitude of this change (Isphording, pers. comm.). Isphording and Flowers (1980) reexamined the Citronelle in Alabama and Mississippi and suggested that it represents the reworking, largely as a result of this uplift, of older deposits. And regardless of precise interpretations, the Miocene uplift surely had profound effects on the directions and flow rates of the then-extant watercourses. Equally, the uplift would have had significant impact on the nature of the gravels and patterns of their deposition.

Alt's (1974) opinions on drainages and the Miocene in general were given considerable weight when Hobbs (1981) speculated about phylogeny. In reviewing the development of the Cambaridae, Hobbs overlooked, possibly deliberately, an important part of Alt's thesis: an arid Miocene. An arid climate would reduce flow of streams and promote emergence of forms adapted to lentic situations. Contrarily, however, the same climate would impede dispersal of crawfishes still adapted to lotic situations. Reduced stream flow would produce a saline intrusion into estuaries. *Procambarus (Ortmannicus) acutus acutus* (Girard) and *P. (Scapulicambarus) clarkii* (Girard) are among the very few species with any saline tolerances; thus, the dispersal of cambarines would be effectively blocked in tidewater areas. The overland route would likewise be impaired, leaving only stream capture as a mechanism for invading new river systems.

Fortunately, however, Alt's thesis can be seriously questioned. Isphording (1970) noted that epidote, garnet, and hornblende, although present only a short distance away, are absent from the Kirkwood Formation and Cohansey Sand of the Middle and Upper Miocene in New Jersey. Otherwise, he found that the remaining heavy mineral species,

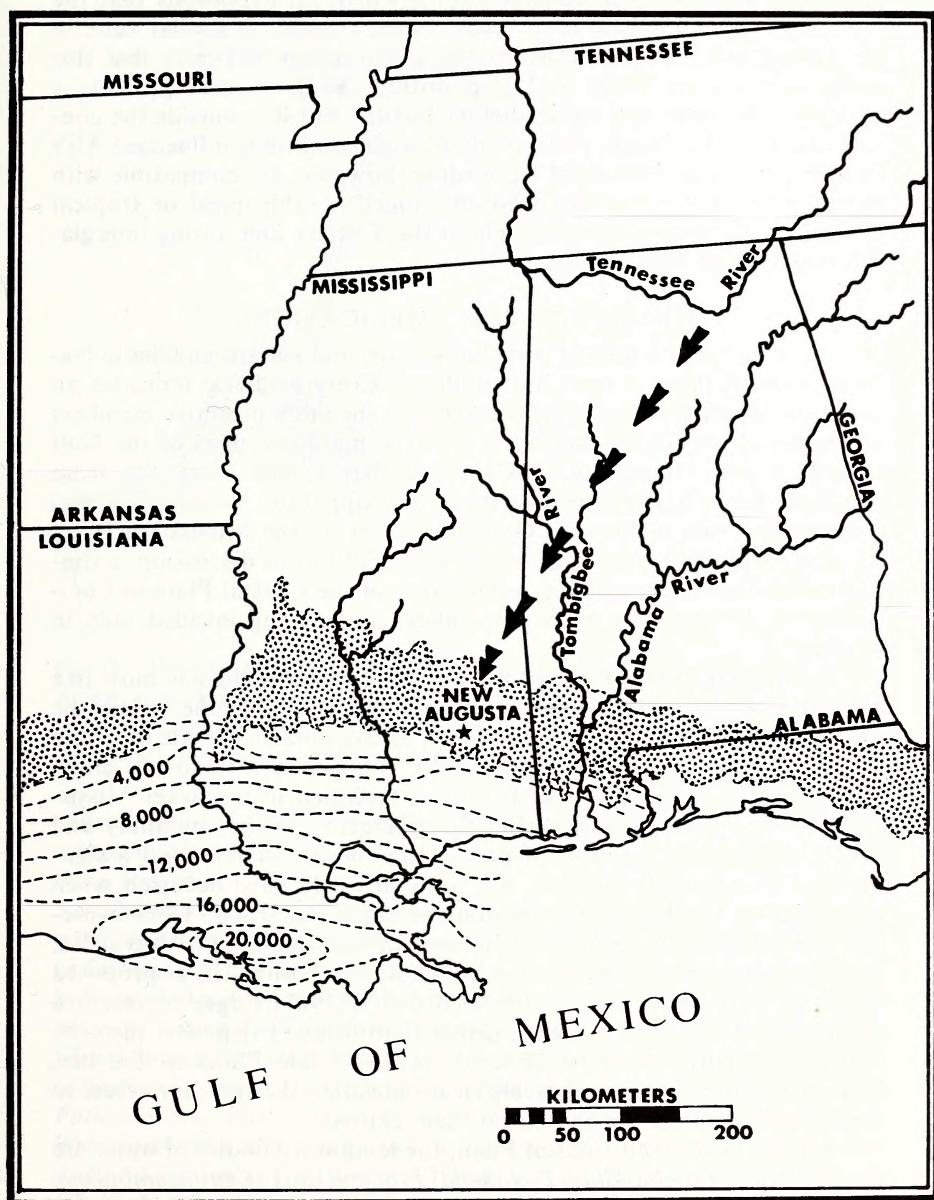


Fig. 6. "Ancestral" Tennessee River" (arrows) of Ispording (1983). (Reproduction of his Fig. 10, p. 303.) Stippling delimits Miocene outcrop.

less susceptible to weathering, were present in expected amounts. This, plus other mineralogical considerations, led to an hypothesis that the period was characterized by a warm, moist climate. A similar suite in the comparable Pascagoula-Hattiesburg Formation indicates that this area, too, was far from arid (Isphording 1983). Florida presents a somewhat different and contradictory picture, but it is outside the considerations of this paper; presumably Florida conditions influenced Alt's thinking. The conclusions of Isphording, however, are compatible with the position of Dorf (1960) who envisioned a subtropical or tropical climate on the Gulf Coast throughout the Tertiary and during interglacial stages of the Pleistocene.

ZOOGEOGRAPHIC IMPLICATIONS

Turning now to animal distribution, we find certain enigmatic features. One of these is the Cambarellinae. Every evidence indicates an early divergence from cambarine stock. Yet the more primitive members of the genus are found associated with the marginal areas of the Gulf Coastal Plain. Fitzpatrick (1983) noted that almost every site from which the genus has been collected in Mississippi (and Florida/Georgia) is south and east of Brown's (1967) ridges or on the Mississippi River flood plain (Fig. 7). Although not as pertinent to this discussion, a similar restriction to geologically recent areas of the Coastal Plain in Louisiana and Texas exists, with deep inland areas being invaded only in Mexico.

Fitzpatrick (1983) believed the ancestral cambarellid was most like *Cambarellus puer* Hobbs and its relatives; but among the species he considered as candidates for this status, all are outside the site of origin for the Cambaridae proposed by Hobbs. Quite clearly, the dwarf crawfishes arose from a stock that became established in the lower Mississippi River lowlands shortly after the emergence of the subfamily and before much diversification of populations began. A temporal assignment of this event is difficult, but it could easily have occurred when proposed by Hobbs (late Cretaceous or early Cenozoic). Their subsequent diversification and expansion east of the Mississippi River delta, however, could not have occurred before Miocene times. If, as proposed by Isphording and Flowers (1983), Brown's (1967) ridges represent a reworking of Miocene deposits, rather than primary deposits, then the eastward expansion is post-Miocene, probably late Pliocene. Further, their distributions give a relatively clear indication that no easy access to lentic habitats of the upper Coastal Plain existed.

On the lower Gulf Coastal Plain, the temporary bodies of water are dominated by *Cambarellus*, *Faxonella*, *Procambarus* (*Capillicambarus*), *P. (Scapulicambarus) clarkii*, and the ubiquitous, probably multi-species taxon, *P. (Ortmannicus) acutus acutus*. All are tertiary burrowers. They are complemented, often sympatrically, by primary burrowers of *Falli-cambarus*, *Cambarus* (*Lacunicambarus*), *Procambarus* (*Acucauda*), and *P. (Hagenides)*. The upper Coastal Plain and inland areas have an

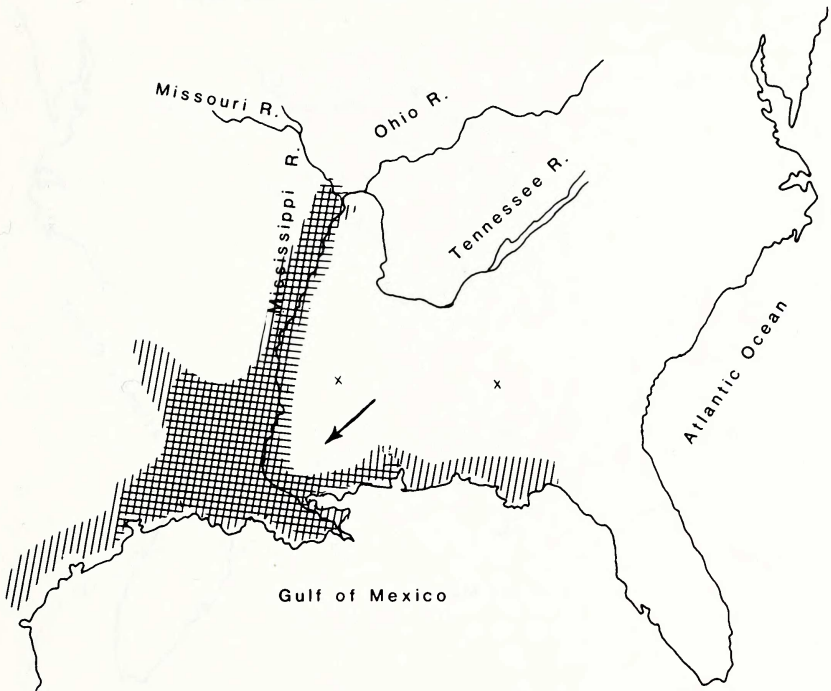


Fig. 7. Distribution of non-Mexican *Cambarellus*. (After Fitzpatrick 1983.) Arrow as in Figure 1. Horizontal ruling = subgenus *Dirigicambarus*; vertical rulings = subgenus *Pandicambarus*; crosses indicate small allopatric, probably introduced, populations of *Cs. (D.) shufeldtii*.

entirely different fauna in these habitats, and the latter two faunae are more closely related to each other than either is to the lower Coastal Plain species.

Procambarus (Capillicambarus) and most of *Fallicambarus* are west of the area in question. *Procambarus (C.) hinei* (Ortmann) occurs as far east as the Florida Parishes of Louisiana, but most of the distribution of the subgenus is in Louisiana and Texas. The range of the more primitive *Fallicambarus* suggests origin of the genus west of the Mississippi River with expansion from there. *Fallicambarus fodiens* is widespread, occurring from lower Ontario to Arkansas and Alabama. *Fallicambarus uhleri* is a species of the Atlantic Coastal Plain, and *F. horton*i Hobbs and Fitzpatrick is apparently of restricted distribution north of the lower Gulf Coastal Plain (Fig. 8). *Fallicambarus hedgpethi* (Hobbs) scarcely crosses to the east bank of the Mississippi River above the delta region, but it can be found in relatively recent deposits all the way to southwestern Georgia. The latter species and *F. fodiens* require thorough taxonomic study before firm conclusions about their distributions can be made.

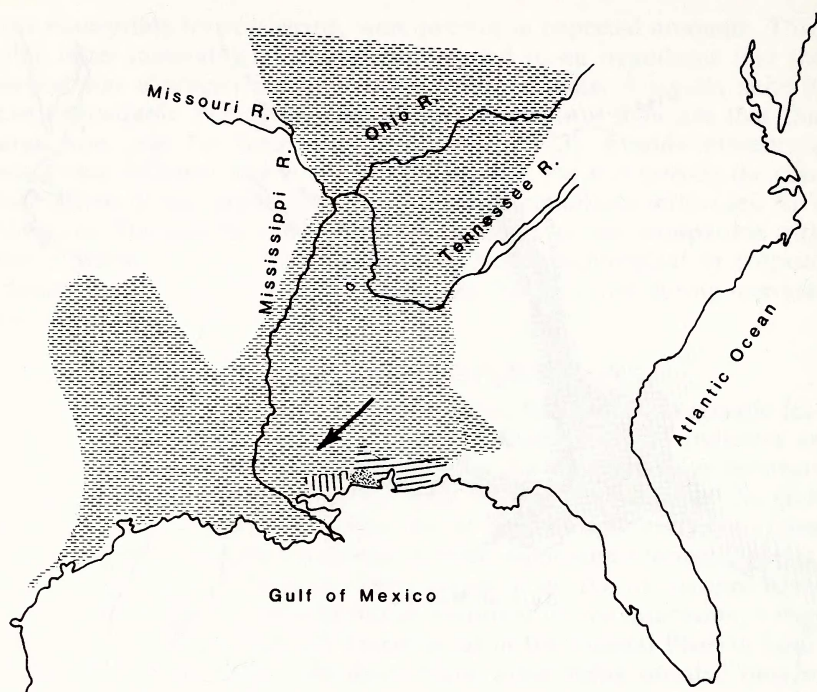


Fig. 8. Distribution of *Fallicambarus* (excluding *F. uhleri*). Arrow as in Figure 1. Horizontal rulings = *F. byersi*; vertical rulings = *F. oryktes*; stippling = *F. danielae*; enclosed by open circle = *F. hortonii*.

Fallicambarus oryktes (Penn and Marlow) is found in the Florida Parishes of Louisiana and along the Mississippi coast. Its eastern limits abut the western limits of the morphologically and ecologically distinctive *F. byersi* (Hobbs). The latter taxon probably represents more than one species, but this does not interfere with the geographic interpretations; the populations occur as far east as the Yellow River basin in Florida. As does *F. oryktes*, it (they) occurs in the immediate vicinity of the coast, rarely penetrating more than 100 km inland. *Fallicambarus danielae* Hobbs is similarly distributed, but apparently it is geographically sympatric with the respective extremes of the two earlier-mentioned species in the central part of the coast. Thus, the spread of these taxa seems to be an event of the late Pliocene or early Pleistocene (Fig. 8). I am not prepared here to discuss the factors that led to establishment of other species of the genus, except to note that the genus and at least some species probably are the result of pre-Pliocene events.

Faxonella probably began in the environs of central Louisiana, where one finds the greatest diversity and the apparently most primitive forms. Indeed, only *Fx. clypeata* (Hay) is widely distributed, and it is found restricted to post-Eocene areas of Alabama and Mississippi in

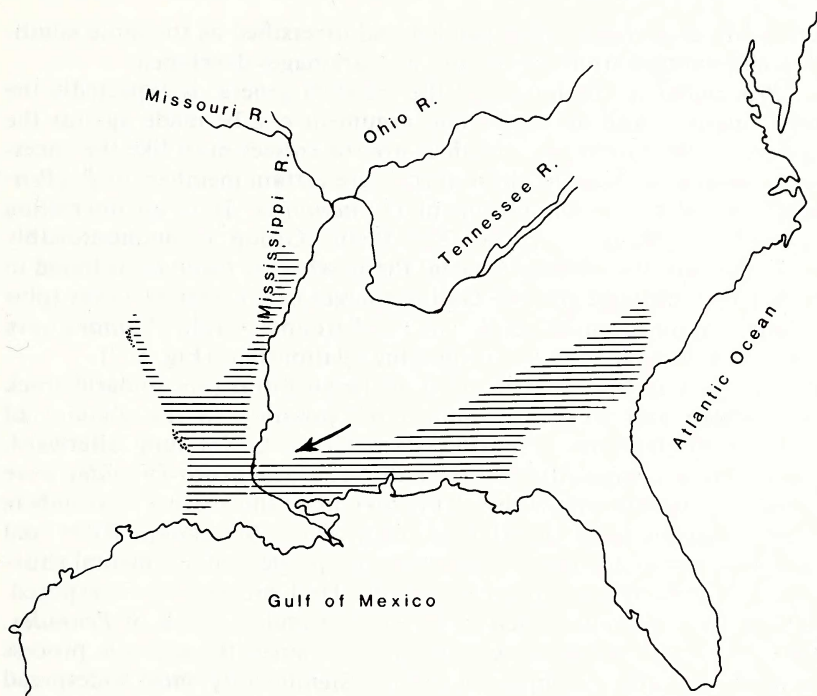


Fig. 9. Distribution of *Faxonella*. Arrow as in Figure 1. Horizontal rulings = *Fx. clypeata*.

that part of its range (Fig. 9). Other, apparently later-differentiating species of other taxa, which have similar environmental habits and cohabit successfully with *Faxonella* elsewhere, are not so widely distributed. Thus, such a distribution as exhibited by *Fx. clypeata*, a relatively advanced member of the genus, argues for an Eocene origin for the genus.

Hobbseus orconectoides Fitzpatrick and Payne, the most primitive member of that genus, occurs in streams associated with Midway (Paleocene) deposits (Fig. 10). The other species occur up and down the Tombigbee drainage, except for one just across the divide in the headwaters of the Pearl drainage. As May (1981) and Murphey and Grissinger (1981) suggested that surface materials analyzed by Grim (1936) represent post-Eocene alluvium rather than primary deposits, the above areas could easily be considerably younger than proposed. One cannot escape the close relationship between *H. orconectoides* habitat and the delta of Grim's (1936) "river of considerable size" or "late Eocene" (probably Miocene). The intimate association of the genus with the Tombigbee drainage makes one suspect that some members of the archiorconectoid stock became isolated in the lower reaches of the river

during Miocene times and expanded and diversified as the more southern lands emerged from the sea and new drainages developed.

Procambarus, the largest of the crawfish genera, is expectedly the most complex. And no significant argument can be made against the supposition that among its members are the species most like the ancestral Cambarinae. Equally, those species are certain members of *P. (Pennides)* and of the Pictus Group of *Ortmannicus*. Here an interesting geographic dichotomy occurs. The Pictus Group is unquestionably associated with the Atlantic Coastal Plain, whereas *Pennides* is found in the Atlantic drainage and the Gulf drainages as far west as Texas (plus an isolate in northern Mexico). The two "groups" within *Pennides* have been noted, as have been the geographic relationships (Fig. 1, 2).

I suggest a very early isolation of the ancestral procambarid stock into eastern and western populations, possibly in the vicinity of northeastern Alabama or northwestern Georgia. Not long afterward, possibly by the large Midway river of Grim, the proto-*Pennides* were divided. Fitzpatrick and Hobbs III (1968) noted the absence of members of the subgenus from the alluvial plain of the Mississippi River and suggested that such a feature, which denies proper environmental situations, is as effective a barrier as if a dry-land bridge were interposed. Perhaps such a barrier acted to isolate a primitive stock of *Pennides*. During Miocene times the western stock retained the cephalic process but diversified into a complex of species. Significantly, most widespread members are west of the Mississippi River, but *P. (Pe.) vioscai* and *P. (Pe.) ouachitae* have variants on the east side. Recently, Hobbs, Jr., and I have discovered what appears to be a population of *P. (Pe.) elegans* Hobbs on the east side, but that species seems to be of limited distribution on both sides of the river. *Procambarus (Pe.) ablusus* Penn is essentially isolated in western Tennessee. The siblings, *P. (Pe.) clemmeri* and *P. (Pe.) penni*, are found south of the "river" of Brown (1967), indicating their divergence and spread occurred no earlier than the Pliocene. The other Mississippi species, *P. (Pe.) lagniappe* Black and *P. (Pe.) lylei* Fitzpatrick and Hobbs, seem to be very restricted, regional isolates.

Farther eastward are the species of *Pennides* that lack a cephalic process. For these, Hobbs's (1981:36-38, 53-54) arguments seem valid. The two enigmas to me are *P. (Pe.) petersi* Hobbs and *P. (Pe.) versutus* (Hagen), both of which have a cephalic process. Otherwise, *P. (Pe.) petersi* is close to *P. (Pe.) raneyi* Hobbs, morphologically and geographically. Perhaps this is indicative that the eastern proto-*Pennides* retained for a short while the cephalic process, but most populations lost it early. Surely the most difficult to interpret is *P. (Pe.) versutus*. Hobbs (1981:38) said, "Considering the Georgia representatives of *Pennides* alone, clearly the most disjunct of the five is *Procambarus versutus* . . ." I concur, but add that it is different from all other *Pennides*, too. It shares many characteristics with the highly restricted *P. (Pe.) lylei*. Both have a distinct shoulder on the cephalic surface of the male

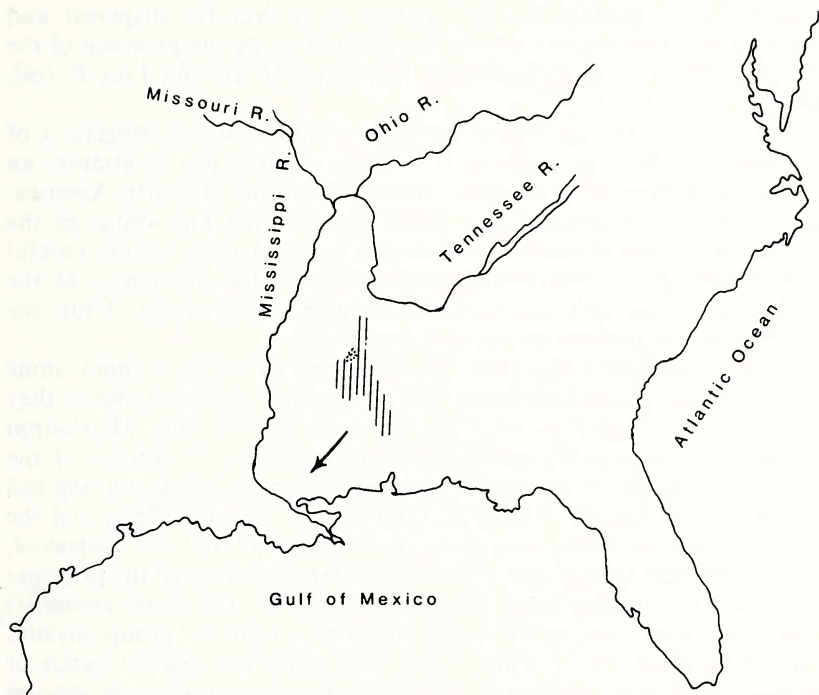


Fig. 10. Distribution of *Hobbseus*. Arrow as in Figure 1. Stippling = *H. orconectoides*.

pleopod; the appendage in each has an attenuated tip; and both have a carinate rostrum. Several western species have caudal projections of the sternite just anterior to the annulus, which partially obscure the receptacle, but none is developed in the same way or to the degree as is the case in *P. (Pe.) versutus*. It is unique in the subgenus in retaining a strong spine on the basis of the cheliped. Despite considerable geographic variation, the species stands alone. It is confined to areas younger than Grim's (1936) "Eocene." Does it represent a third line of proto-*Pennides* descendants, is it a Miocene phenomenon, or is it both of the preceding?

Moving to a second subgenus of *Procambarus*, *Scapulicambarus*, another pattern related to post-Miocene development can be seen. Only *P. (S.) clarkii* (and one other, below) is found significantly outside the southern Atlantic Coastal Plain or the Flint-Chattahoochie basin (Fig. 11). The easternmost limit of this species is in Escambia County, Florida, and where it traverses the coast it is in post-Miocene areas. Again, its dispersal seems to be a post-Miocene event. As its relatives are all in the extreme southeastern United States, an origin in that area is not unreasonable. Equally, a post-Miocene origin is feasible. But since the species has spread as far as Mexico (Hobbs 1962b) in such a

short time, it becomes a very interesting subject for dispersal and competition studies. The question is complicated by the presence of the relatively primitive *P. (S.) strenthi* Hobbs (1977) in San Luis Potosí, Mexico.

Numerous other problems exist in the undiscussed subgenera of *Procambarus*. But the purpose of this treatment is not to attempt an exhaustive resolution of zoogeographical situations of North America. Instead, it is to emphasize that more sophisticated knowledge of the geology of an evolutionarily critical area can and does require careful reflection on prior conclusions with respect to the phylogeny of the animals, and especially the temporal assignments of events. Thus, the specific answers are best left to other studies.

The discussion would not be complete, however, without some mention of the genera *Cambarus* and *Orconectes*. As noted above, they both are poorly represented in the area of the old Mississippi Embayment. Until more is known of the precise relationships of the several populations of *Cambarus (Lacunicambarus)* almost nothing can be said of their history. This was recognized by Hobbs (1969), and the only progress thus far has been the description of two restricted, peripheral species (Fitzpatrick 1978, Hobbs 1981), leaving all the principal questions still unanswered. Otherwise, only *C. (Depressicambarus) striatus*, an "advanced" member of a "relatively primitive" group, invades to the Mississippi River. Particularly important here are the habits of this species. I have observed individuals moving across open ground when the humidity is only moderately high, and I have found their burrows on hillsides somewhat removed from flowing or standing surface water. Surely, this species is not as restricted in its dispersal as are many others.

Orconectes is represented by no relatively primitive species. Although the exact relationships of the taxa are presently undetermined, I am sufficiently progressed in a monographic study of the genus to be comfortable with the concept that the area in question is populated by relatively advanced forms. Many are members of the Palmeri Group; they probably represent an invasion from the west. Most of the remainder are Virilis Section species, which probably represent an eastern assemblage expansion. The striking feature is the absence of simple, less advanced forms.

Hobbs's (1967, 1981, 1983) arguments in favor of an early divergence of procambarid-like stocks are quite sound. Equally, his ideas of the emergence of proto-*Cambarus* and proto-*Orconectes* cannot be faulted. The paradox exists in the geological data that suggest a large Midway-time river from the southern Appalachians, entering the Mississippi Embayment in the area near the headwaters of the present Pearl River (Grim 1936). Another strong river reworked the "Citronelle" deposits and emptied just north of Lake Pontchartrain (Brown 1967). Current dating would place these events in late Miocene or early Pliocene.

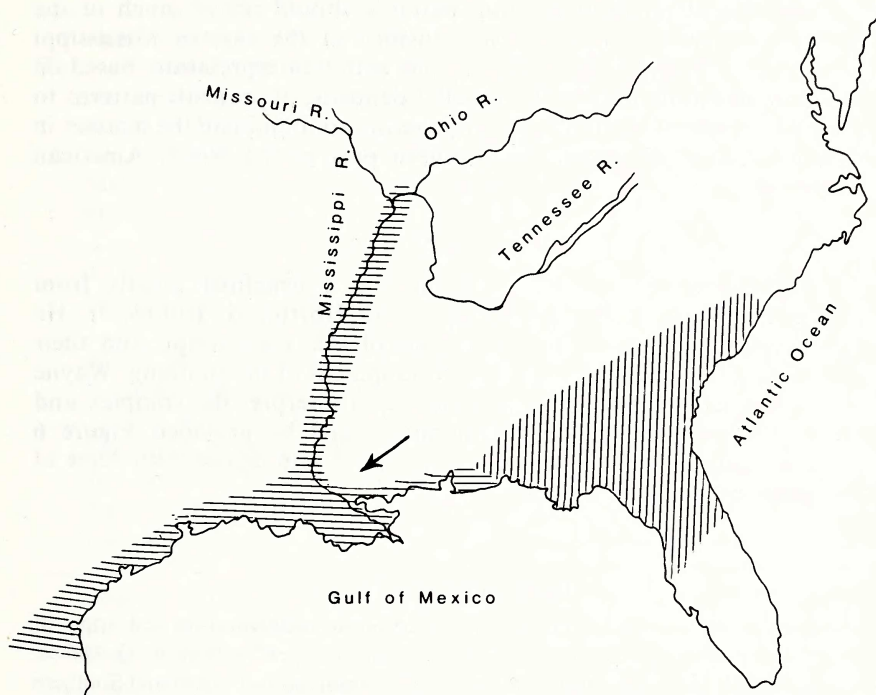


Fig. 11. Distribution of *Procambarus (Scapulicambarus)*. Arrow as in Figure 1. Horizontal rulings = *P. (S.) clarkii*.

Mineralogic data argue strongly that the southern Appalachian highlands had a significant role in contributing to sediments of the central Gulf Coastal Plain, probably via a major river—the “upper” Tennessee—until late Pliocene times (Isphording 1983).

It is difficult to imagine that a vigorous *Cambarus* and *Orconectes* stock established in the southern Appalachians or on the Cumberland Plateau would not exploit this route (or routes) for the invasion of the newly emerging habitats. Thus, either the two genera were well established and diversified by the end of the Miocene or they did not emerge until Pliocene times. Logic favors the former thesis. Otherwise, crawfishes would be undergoing speciation at a rate not supported by any other evidence.

A Miocene intrusion in Mississippi to within 50 km of the Tennessee boundary (May 1981, Murphey and Grissinger 1981) is a significantly different situation than previously assumed. As Murphey and Grissinger (1981) indicated, the Eocene (and probably subsequent) drainage patterns have been buried. Surely, the influential Miocene uplift had profound effects on the freshwater drainage. A very fruitful area for study exists in Alabama and Mississippi. Detailed analysis of

the specifics of microdistribution patterns should reveal much of the geologic, as well as the faunistic, history of the eastern Mississippi Embayment. Correlation of these results with reinterpretation, based on the more recent datings of "Citronelle" deposits, of faunistic patterns to the east or west of the Embayment promises to illuminate the manner in which aquatics populated the southern part of the North American continent.

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